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*Published in:*  
Journal of Experimental Marine Biology and Ecology

*DOI:*  
[10.1016/j.jembe.2008.03.011](https://doi.org/10.1016/j.jembe.2008.03.011)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2008

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Compton, T. J., Kentie, R., Storey, A. W., Veltheim, I., Pearson, G. B., & Piersma, T. (2008). Carbon isotope signatures reveal that diet is related to the relative sizes of the gills and palps in bivalves. *Journal of Experimental Marine Biology and Ecology*, 361(2), 104-110. <https://doi.org/10.1016/j.jembe.2008.03.011>

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## Carbon isotope signatures reveal that diet is related to the relative sizes of the gills and palps in bivalves

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### ARTICLE INFO

#### Article history:

Received 15 August 2007

Received in revised form 24 March 2008

Accepted 25 March 2008

#### Keywords:

$\delta^{15}\text{N}$

$\delta^{13}\text{C}$

Bivalve

Gill

Morphospace

Palp

Stable isotopes

Trait

### ABSTRACT

In marine bivalves, the relative sizes of the gills and palps appear to be a useful functional trait that reflect feeding mode, i.e. suspension feeders have relatively larger gills than palps for pumping, whereas deposit feeders have relatively larger palps than gills for sorting. Also, within a species, the relative sizes of the gills and palps are related to changes in local food conditions. However, there is still no firm evidence showing that differences in the relative gill and palp sizes between species are related to diet selection. Based on the knowledge that carbon and nitrogen isotope signatures of an animals tissues reflect past diet, we compared the relative gill and palp sizes of bivalves from Roebuck Bay, northwestern Australia with their carbon and nitrogen isotope signatures. The carbon isotope signatures distinguished clear differences in diet between bivalves along a gradient from suspension to deposit feeding, and strikingly this pattern was closely followed by the relative sizes of the gills and palps of the bivalves. This study confirms that relative gill and palp sizes in bivalves are a functional trait that can be used to compare resource use between species. Furthermore, these data may suggest that morphospace occupation, as determined by relative gill and palp sizes of bivalves, could reflect a gradient of resource use between species.

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### 1. Introduction

Functional traits have been proposed as necessary building blocks needed to provide insights into species adaptations and interactions including ecosystem properties (McGill et al., 2006). A trait is defined as any morphological, physiological or phenological feature measurable at the level of the individual, and a functional trait is a trait that impacts fitness indirectly via its effects on growth, reproduction or survival (Violle et al., 2007). It is expected that the most predictive functional traits will be those that relate directly to resource acquisition (McGill et al., 2006), e.g. beak size and shape in birds (Schoener, 1971) and feeding morphology in fishes (Bellwood et al., 2006). A revival of trait comparisons in community ecology should be useful (McGill et al., 2006); as previously, morphological traits have provided insights both as direct and indirect measures of an organism's performance and/or resource use (Wainwright, 1994).

Contrary to the expectation that benthic bivalve species indiscriminately select their diet based solely on the size of food particles (see review by Ward and Shumway, 2004), there is evidence to show that bivalve species have the potential to select their diet based on particle quality via their feeding processes (Levinton et al., 1996; Ward and Shumway, 2004; Ward et al., 1997). Feeding processes, i.e. food uptake and selection, are optimized by the finely-tuned cooperation between the gills (ctenidia) and labial palps of the bivalves. The main role of the gills is to trap particles from a self-generated water current, and transfer these particles to the labial palps (Jones et al., 1992; Meyhöfer, 1985; Møhlenberg and Riisgård, 1978). The labial palps predominantly sort the organic from inorganic particles (Pohlo, 1967; Yonge, 1949). Organic particles are then accepted into the alimentary canal, whereas inorganic particles are rejected as pseudofaeces. Depending on the gill type in some suspension feeders sorting and rejection of particles can take place on the gill and the role of the labial palps can be reduced (Barille et al., 2000; Dutertre et al., 2007; Shumway et al., 1985; Ward et al., 1998). Interestingly, the way in which bivalves deal with food quantity and quality appears to be species dependent (Ward et al., 2003).

The capability of the gills and palps to respond to food conditions and distinguish bivalve feeding modes, suggests that these organs are a unique functional trait. Within a species, the size of the gills and labial palps are

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**Table 1**

Species names, their authority name (authority) and their phylogenetic classification (subclass, order, superfamily, family)

species	authority	subclass	order	family	MGS	silt	description of habitat	latitude	longitude
<b>Suspension feeders</b>									
<i>Anadara granosa</i>	Linnaeus 1758	Pteriomorphia	Arcoidea	Arcidae	96	28	DF: fine sediments	–17°58'36"	122°16'16"
<i>Anomalocardia squamosa</i>	Linnaeus 1758	Heterodonta	Veneroidea	Veneridae	168	8	DF: sandy sediments	–17°58'43"	122°15'22"
<i>Barbatia pistachio</i>	Lamarck 1819	Pteriomorphia	Arcoidea	Arcidae	NA	NA	DF: rocky outcrop	–17°58'54"	122°16'05"
<i>Gafrarium tumidum</i>	Röding 1798	Heterodonta	Veneroidea	Veneridae	163	8	DF: mangrove roots	–17°58'50"	122°16'12"
<i>Placamen berryi</i>	Menke 1843	Heterodonta	Veneroidea	Veneridae	103	23	DF: fine sediments	–17°58'47"	122°16'47"
<b>Deposit feeders</b>									
<i>Tellina capsoides</i>	Lamarck 1818	Heterodonta	Veneroidea	Tellinidae	88	30	DF: fine sediments	–17°58'47"	122°16'47"
<i>Tellina</i> sp.		Heterodonta	Veneroidea	Tellinidae	23	85	One Tree: silt	–17°59'24"	122°22'58"
<i>Tellina piratica</i>	Hedley 1918	Heterodonta	Veneroidea	Tellinidae	168	8	DF: sandy sediments	–17°58'43"	122°15'11"
<b>Lucinid bivalve</b>									
<i>Divercella irpex</i>	Smith 1885	Heterodonta	Veneroidea	Lucinidae	117	22	DF: sandy sediments	–17°58'47"	122°15'14"

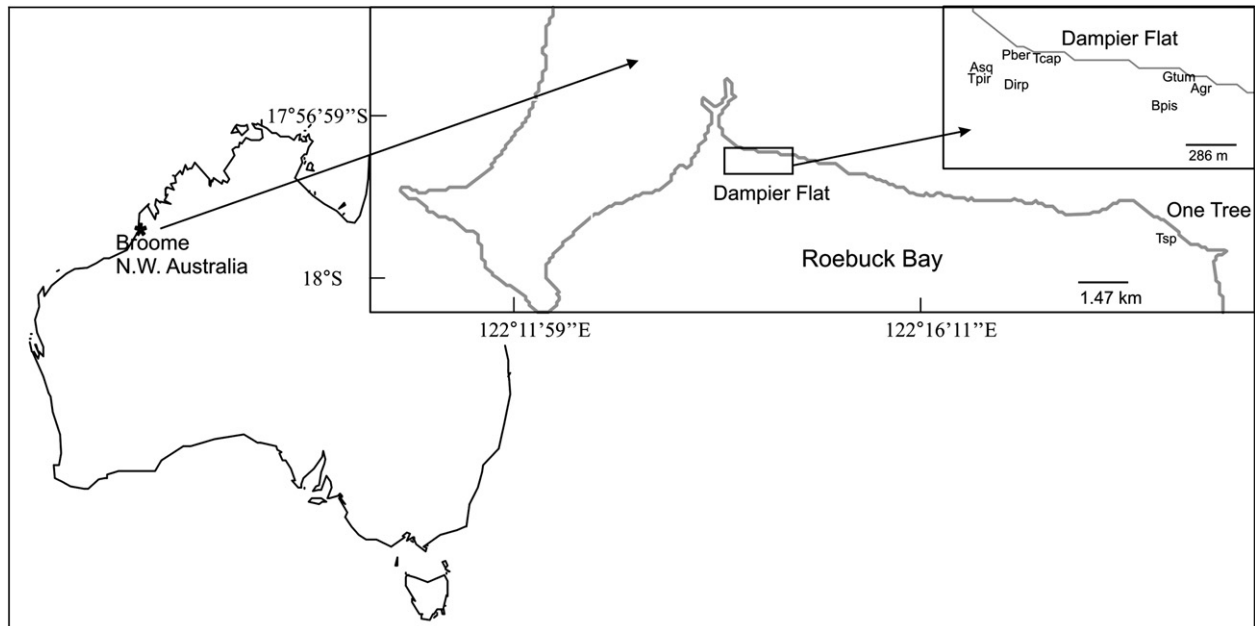
The sediment characteristics measured at the sample site of each species are included: median grain size (MGS) and silt (<63 µm fraction of sediment, %) and a description of the habitat (DF is Dampier Flat). The geographical coordinates of collection are also included. NA indicates data was not available.

known to be flexible (Drent et al., 2004; Piersma and Drent, 2003) and related to changing food conditions over time (Honkoop et al., 2003) and space, e.g. turbidity and silt (Barille et al., 2000; Drent et al., 2004; Essink et al., 1989; Payne et al., 1995a; Payne et al., 1995b; Theisen, 1982). Furthermore, the relative size of the gills and labial palps reflect different functional roles in suspension and deposit feeding bivalves. In suspension feeders, the relatively larger gills than labial palps suggest pumping is important for food collection (Jones et al., 1992; Møhlenberg and Riisgård, 1978), whereas in deposit feeders the relatively larger labial palps than gills suggest sorting is important for purging inorganic material (Pohlo, 1967; Reid and Reid, 1969; Yonge, 1949). Interestingly, the relative size of the gills versus the labial palps in multiple bivalve species form a gradient between suspension and deposit feeders within two tidal flat systems, suggesting that bivalves can fill a wide spectrum of feeding niches (Compton et al., 2007). Thus, relative gill and palp sizes of bivalves are known to relate to food acquisition. However, there is no direct evidence showing that the relative gill and palp sizes reflect diet selection.

Previously, it was not easy to identify how feeding morphology was related to diet in bivalves because: (1) assimilated food sources were difficult to determine (Hummel, 1985; Kamermans, 1994), and (2) some bivalve species easily switch feeding mode, e.g. facultative deposit feeders

(Brafeld and Newell, 1961; Hughes, 1969; Ólafsson, 1986; Peterson and Skilleter, 1994; Thompson and Nichols, 1988). For example, stomach content analysis suggested that a suspension (*Cerastoderma edule*) and a deposit (*Macoma balthica*) feeder were eating similar proportions of the same food sources, i.e. benthic and pelagic algae (Kamermans, 1994). More recently, carbon and nitrogen stable isotopes have shown a clear-cut separation between bivalve species in their assimilated carbon sources (viz. dietary sources) (Decottignies et al., 2007b; Herman et al., 2000; Riera, 2007; Riera and Richard, 1996; Riera et al., 1999), such that the suspension feeder (*Cerastoderma edule*) was observed to assimilate carbon from plankton, whereas the deposit feeder (*Macoma balthica*) assimilated carbon from a mixed diet of benthic microalgae and plankton (Rossi et al., 2004). Within individual bivalve species, carbon isotopes have also shown that there is differential diet selection along estuarine gradients (Riera and Richard, 1996; Yokoyama and Ishihi, 2003), and that bivalve diets reflect changing food conditions over time (Decottignies et al., 2007a; Decottignies et al., 2007b).

In this study, the gill and palp size of bivalves were related to the carbon and nitrogen isotope signatures of the bivalves from Roebuck Bay, northwestern Australia. We aimed to test whether the relative sizes of gills and palps of bivalves reflect diet, and thus can be used as a functional



**Fig. 1.** Roebuck Bay is situated near the town of Broome. Within Roebuck Bay the study sites were Dampier Flat and One Tree. Within the sample site of Dampier flat, the sample spot of each bivalve species is indicated. The species names are abbreviated: Asq – *A. squamosa*, Gtum – *G. tumidum*, Pber – *P. berryi*, Agr – *A. granosa*, Bpis – *B. pistachia*, Tsp – *T. sp.*, Tcap – *T. capsoides*, Tpir – *T. piratica*, Dirp – *D. irpex*.

trait for interspecies comparisons. Possible food sources were characterized using carbon and nitrogen isotopes and related to the isotopic signatures of the sampled bivalve species.

## 2. Materials and Methods

### 2.1. Collection methods

The field work for this study was carried out in the first two weeks of November 2003. Bivalves were collected from Dampier Flat, located on the tidal flat of Roebuck Bay, northwestern Australia (17°S and 122°E). The site is fringed by mangrove trees (*Avicennia marina*, *Rhizophora* sp.), and has tidal ranges that vary between 3.5 m at neap to 8.5 m at spring tide. The area has a wet–dry tropical climate, with a warm, dry season from May to November, followed by a hot, monsoonal–influenced wet season, with most rain arising from cyclonic activity (Rogers et al., 2003). In Roebuck Bay, chlorophyll–a values are generally low and average about  $0.7 \pm 0.4$  mg/l; measured over a three year period (Rose et al., 1990).

Aiming to sample a variety of feeding modes, we specifically chose adults of five suspension feeding bivalve species (*Anadara granosa*, *Placamen berryi*, *Anomalocardia squamosa*, *Barbatia pistachia*, *Gafrarium tumidum*), three deposit feeding bivalve species (*Tellina capsoides*, *T. piratica* and *Tellina* sp.) and a lucinid bivalve (*Divaricella irpex*) for morphological and stable isotope analyses. One tellinid species (*Tellina* sp.) was sampled from another location on the tidal flat (One Tree). Species were sampled based on the knowledge of bivalve distributions (Pepping et al., 1999). Sampling was completed outside of the main reproductive period of the bivalve species concerned (de Goeij et al., 2003, R. Kentie pers obs). For more detail on the sampling location, and sediment parameters at the point of bivalve species collection, please see Table 1 and the map of sampling points in Fig. 1.

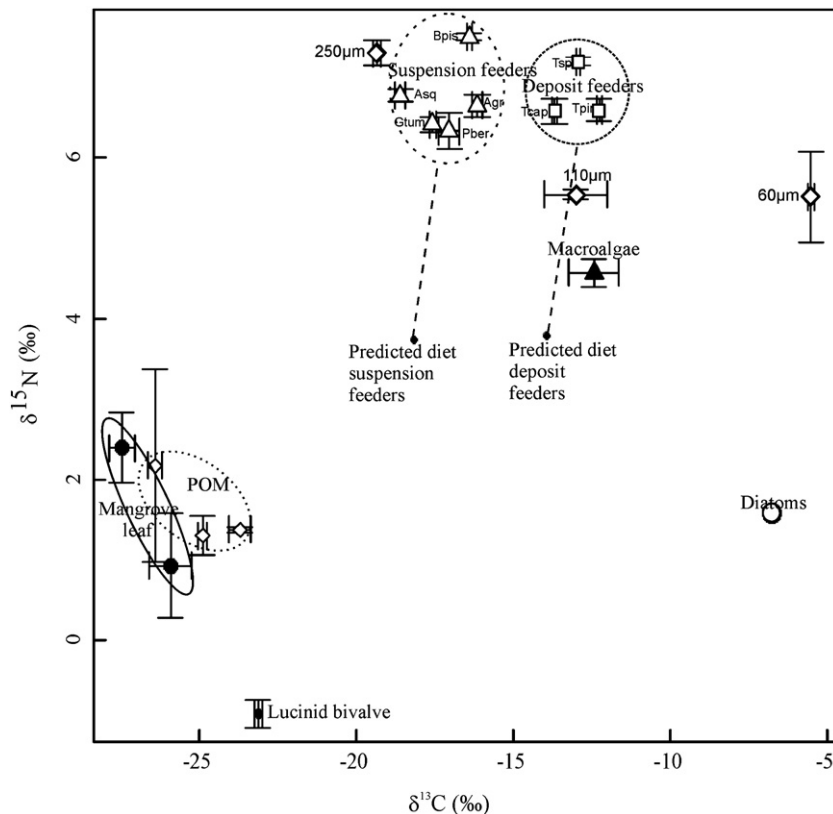
Morphological and stable isotope analyses were completed on the same individual in all cases ( $n=3-5$  individuals per species), allowing direct comparison within individuals. The lucinid species was not analysed for its morphology, as it has modified gills and palps (Beesley et al., 1998) that are likely to host endosymbiotic bacteria (Taylor and Glover, 2006). All species dwell within the sediment, except for *B. pistachia* which is a rocky intertidal species. Specimens were collected by either careful removal from rocks, passing sediment through a 1–mm sieve, or digging in the mud with hands. After collection all species were placed in ultra-violet irradiated filtered seawater for 48 hours to allow for depuration, prior to dissection.

### 2.2. Bivalve feeding morphology

It has been established that the mass of the gills and palps are an accurate measure of the size of these three–dimensional organs (Honkoop et al., 2003; Drent et al., 2004). Therefore gills and palps of bivalves were dissected, using surgical forceps, under a binocular microscope within 48 h of collection. Dissected feeding organs were then placed in platinum crucibles and dried at 60 °C for three days. Following drying, the organs were cooled in a dessicator and weighed to the nearest 0.1 mg (Mettler Toledo AE 160 balance). After weighing, the organs were incinerated at 560 °C for five hours, and left to cool before weighing a second time. The difference between the dried and ashed mass being the ash–free dry mass (AFDM). To observe the variation in feeding morphology between species, we log transformed and ranked the gill–to–palp mass ratios.

### 2.3. Stable isotope analysis

In this study, stable isotopes of both carbon and nitrogen were measured, as when primary food sources overlap (Fry and Sherr, 1984;



**Fig. 2.** Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope signatures (with standard error bars) of the nine bivalve species and their potential food sources (mangrove leaf, mangrove particulate organic matter (POM) diatoms, and plankton (250  $\mu\text{m}$  ( $x > 250 \mu\text{m}$ ), 110  $\mu\text{m}$  (250  $\mu\text{m} > x > 110 \mu\text{m}$ ) and 60  $\mu\text{m}$  (110  $\mu\text{m} > x > 60 \mu\text{m}$ )). Note that the species names are abbreviated in the figure (Suspension feeders: Asq – *A. squamosa*, Gtum – *G. tumidum*, Pber – *P. berryi*, Agr – *A. granosa*, Bpis – *B. pistachia* and Deposit feeders: Tsp – *T. sp.*, Tcap – *T. capsoides*, Tpir – *T. piratica*, Lucinid bivalve – *D. irpex*). Macroalgae was rare on the tidal flat. The predicted diets, based on trophic fractionation steps of 1‰ for  $\text{C}^{13}$  and 3.5‰ for  $\text{N}^{15}$ , of the suspension and deposit feeding bivalves are also indicated.

**Table 2**

The mean nitrogen ( $\delta^{15}\text{N}$  ‰) and carbon ( $\delta^{13}\text{C}$ ) isotopic signatures ( $\pm\text{SE}$ ) for the bivalve species sampled at Roebuck Bay, Dampier Flat in November 2003

species	$\delta^{15}\text{N}$	SE	$\delta^{13}\text{C}$	SE	n	Length(mm)	SE
<b>Suspension feeders</b>							
<i>Anadara granosa</i>	6.65	0.14	−16.15	0.15	5	35.22	1.56
<i>Anomalocardia squamosa</i>	6.77	0.08	−18.61	0.17	5	20.83	0.60
<i>Barbatia pistachia</i>	7.50	0.05	−16.41	0.09	4	44.82	3.95
<i>Gafrarium tumidum</i>	6.44	0.07	−17.62	0.09	4	42.80	2.26
<i>Placamen berryi</i>	6.33	0.23	−17.04	0.32	3	22.13	0.99
<b>Deposit feeders</b>							
<i>Tellina capsoides</i>	6.58	0.15	−13.68	0.10	5	37.40	1.12
<i>Tellina</i> sp.	7.20	0.06	−12.91	0.07	5	27.74	0.22
<i>Tellina piratica</i>	6.59	0.14	−12.26	0.10	5	31.51	0.71
<b>Lucinid bivalve</b>							
<i>Divaricella irpex</i>	−0.92	0.17	−23.14	0.12	5	13.88	0.28

The number of bivalves per species sampled (n) and their average shell length ( $\pm\text{SE}$ ) are indicated.

Riera and Richard, 1996; Schwinghamer et al., 1983), or when there are three or more potential food sources, a dual isotope approach has provided the greatest resolution (Peterson and Howarth, 1987). The tissue selected for carbon and nitrogen stable isotope analysis was the foot, except in the case of *B. pistachia* where the adductor muscles were used because the foot muscle is reduced and provides insufficient biomass for analysis. Isotopic ratios should ideally be compared using a single tissue type, as isotope ratios can differ between tissues due to isotopic fractionation and tissue turnover rates (Gannes et al., 1997). The foot muscle was chosen because it is most likely to reflect long-term food assimilation (Peterson and Fry, 1987). In bivalves, it takes approximately 23 days for a new diet to be assimilated into body tissue (Dubois et al., 2007).

During dissection of the feeding organs, the foot or adductor muscles of the bivalves were removed and placed in porcelain crucibles for drying at 60 °C for two days. Following drying, the tissues were ground and homogenized with a mortar and pestle. The ground samples were then weighed (~1.5 to 2.0 mg) into 5-mm tin-foil cups and placed directly into a freezer (−4 °C).

The prepared samples were analyzed with a dual beam atomic absorption spectrophotometer at the University of Western Australia, for their carbon and nitrogen isotope values. All isotope data are expressed in the standard  $\delta$  unit notation:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3, \quad (1)$$

where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  for carbon and  $R = {}^{15}\text{N}/{}^{14}\text{N}$  for nitrogen, relative to the standards of Pee Dee Belemnite for carbon and atmospheric nitrogen for nitrogen.

#### 2.4. Primary food sources

Carbon and nitrogen isotopic signatures were also derived for all apparent primary producers evident on the Dampier Flat location. Mangrove leaves (*Avicennia marina*, *Rhizophora* sp.), and mangrove coarse particulate organic matter (CPOM) were sampled from the fringes of the tidal flat. Mangrove-derived medium and fine particulate organic matter (MPOM and FPOM) were obtained by elutriating sediment samples in a bucket and passing the suspended material through 180  $\mu\text{m}$  and 1 mm mesh sieves. Macroalgae were picked from the tidal flat surface and from objects projecting above the flats (reef outcrops and stakes). Marine 'plankton' (a mixture of phyto- and zooplankton with some seston/detritus) was collected from the water column on an incoming tide using nested plankton nets of three different mesh sizes: (1) 250  $\mu\text{m}$  ( $x > 250 \mu\text{m}$ ), (2) 110  $\mu\text{m}$  (250  $\mu\text{m} > x > 110 \mu\text{m}$ ) and (3) 60  $\mu\text{m}$  (110  $\mu\text{m} > x > 60 \mu\text{m}$ ) that were deployed behind a slow moving boat adjacent to the flats. The

plankton was concentrated onto a Whatmann glass-fiber filter (GF/C) with a vacuum pump, and the filters frozen for storage. At low tide, a brown-green sheen progressively developed across the exposed mud flats, presumed to be diatoms moving to the surface as the tide receded. A two stage process was used to isolate the diatoms. Initially, where the brown-green colour was most strongly developed, the top few mm of material was carefully scraped and concentrated into a container for return to the laboratory. In the laboratory, the sediment was kept moist and covered by GF/C filters with glass cover slips placed on top of the filter. A light gradient was then used to attract the diatoms through the filter and onto the cover slips. The diatoms on the cover-slip were then dried and scraped into a tin-foil crucible. This process was repeated until sufficient mass was collected for isotopic determination ( $n=1$ ).

Preparation and measurement of source material was done using the same methods as the tissue stable isotope analysis, except that the source material was weighed to ~5.5 mg to allow for lower carbon content.

#### 2.5. Analysis

Isotopic mass balance equations were used to estimate the range of possible food sources contributing to the diet of each bivalve species using the Isosource model (Phillips, 2001; Phillips and Gregg, 2003). To estimate the predicted diet values of the bivalves, fractionation values of 1‰  $\delta^{13}\text{C}$  and 3.4‰  $\delta^{15}\text{N}$  were subtracted from the isotopic signatures of the bivalves prior to analysis. These fractionation values have been determined previously in two bivalve species (Yokoyama et al., 2005) and other organisms (Minagawa and Wada, 1984; Rau et al., 1983). In the Isosource model, the diet of each species was calculated from the average isotopic food source values: plankton (60 – 110  $\mu\text{m}$ , 110 – 250  $\mu\text{m}$  and  $>250 \mu\text{m}$ ), diatoms and mangrove material (i.e. POM and mangrove leaf material). Macroalgae were excluded from the model as they are rare on this tidal flat. To test whether nitrogen isotope signatures differed between feeding modes a one-way ANOVA was used. Finally, a linear regression was used to examine whether there was a significant correlation between the log gill-to-palp mass ratio and the  $\delta^{13}\text{C}$  ratios of the bivalves.

### 3. Results

At Roebuck Bay, the bivalve species were clearly differentiated into three groups based on their carbon isotope signatures (Fig. 2, Table 2). In contrast, the nitrogen isotope signatures ( $\delta^{15}\text{N}$ ) did not differ between the suspension (from 6.33 to 7.50‰) and deposit feeding modes ( $F_{1,34}=0.075$ ,  $P=0.79$ , from 6.6 to 7.2‰, Table 2). At this site, the suspension feeders had relatively depleted carbon isotope signatures in the range of −16.2 to −17.0‰, and the deposit feeders had more enriched carbon isotope signatures with values in the range of −12.3 to −13.7‰.

**Table 3**

The mean nitrogen ( $\delta^{15}\text{N}$  ‰) and carbon ( $\delta^{13}\text{C}$ ) isotopic signatures ( $\pm\text{SE}$ ) of the possible primary food sources collected at Roebuck Bay, Dampier Flat

source	$\delta^{13}\text{C}$	SE	$\delta^{15}\text{N}$	SE	n
<i>Rhizophora</i> sp. (leaf)	−25.92	0.68	0.93	0.65	3
<i>Avicennia marina</i> (leaf)	−27.49	0.40	2.39	0.44	3
POM (Coarse)	−26.43	0.21	2.18	1.20	3
POM (Medium)	−24.91	0.16	1.30	0.25	3
POM (Fine)	−23.72	0.37	1.38	0.03	3
Macroalgae (green)	−11.04	0.86	4.40	0.18	3
Macroalgae (brown)	−13.81	0.69	4.74	0.29	3
Plankton ( $>250 \mu\text{m}$ )	−19.35	0.10	7.31	0.16	4
Plankton (250 $\mu\text{m} > x > 110 \mu\text{m}$ )	−13.00	1.01	5.54	0.06	3
Plankton (110 $\mu\text{m} > x > 60 \mu\text{m}$ )	−5.51	0.11	5.52	0.56	6
Diatoms	−6.74		1.58		1

In the table n is the number of replicates collected, and POM represent particulate organic matter.



**Table 4**

Mean contributions (% followed by the range in brackets) of the oceanic and tidal flat food sources to the diet of each bivalve species

sp	Bivalve		Bivalve diet		Oceanic plankton			Tidal flat food sources		
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	250 $\mu\text{m}$	110 $\mu\text{m}$	60 $\mu\text{m}$	diatoms	POM	leaf
<b>Suspension feeders</b>										
<i>A. granosa</i>	6.7	-16.2	3.3	-17.2	9.3 (0–3.1)	14.1 (0–45)	15.3 (0–44)	16.3 (0–37)	23.4 (0–59)	21.6 (0–55)
<i>A. squamosa</i>	6.8	-18.6	3.4	-19.6	13.5 (0–33)	16.1 (0–47)	9.5 (0–31)	7.3 (0–25)	26.1 (0–62)	27.6 (0–61)
<i>B. pistachio</i>	7.5	-16.4	4.1	-17.4	19.5 (0–45)	22.1 (0–65)	12.8 (0–39)	9.2 (0–31)	18.1 (0–47)	18.4 (0–46)
<i>G. tumidium</i>	6.4	-17.6	3.0	-18.6	7.8 (0–26)	11.7 (0–37)	12.3 (0–37)	14.3 (0–32)	28.2 (0–67)	25.8 (0–62)
<i>P. berryi</i>	6.3	-17.0	2.9	-18.0	7.2 (0–24)	10.8 (0–35)	11.5 (0–35)	19 (1–36)	27 (0–64)	24.5 (0–59)
AVERAGE					11.46 $\pm$ 5.12	14.96 $\pm$ 4.5	12.28 $\pm$ 2.11	13.22 $\pm$ 4.88	24.56 $\pm$ 4.02	23.58 $\pm$ 3.63
<b>Deposit feeders</b>										
<i>T. capsoides</i>	6.6	-13.7	3.2	-14.7	8.6 (0–29)	13.2 (0–43)	14.9 (0–43)	30.6 (11–50)	17.1 (0–46)	15.6 (0–42)
<i>T. piratical</i>	6.6	-12.3	3.2	-13.3	8.4 (0–29)	13.1 (0–43)	15.4 (0–43)	37.6 (18–57)	13.3 (0–39)	12.2 (0–35)
<i>T. sp.</i>	7.2	-12.9	3.8	-13.9	11.1 (0–40)	17.7 (0–58)	22 (0–58)	23.4 (0–51)	13.5 (0–43)	12.3 (0–39)
AVERAGE					9.37 $\pm$ 1.5	14.67 $\pm$ 2.63	17.43 $\pm$ 3.96	30.53 $\pm$ 7.10	14.63 $\pm$ 2.14	13.37 $\pm$ 1.93

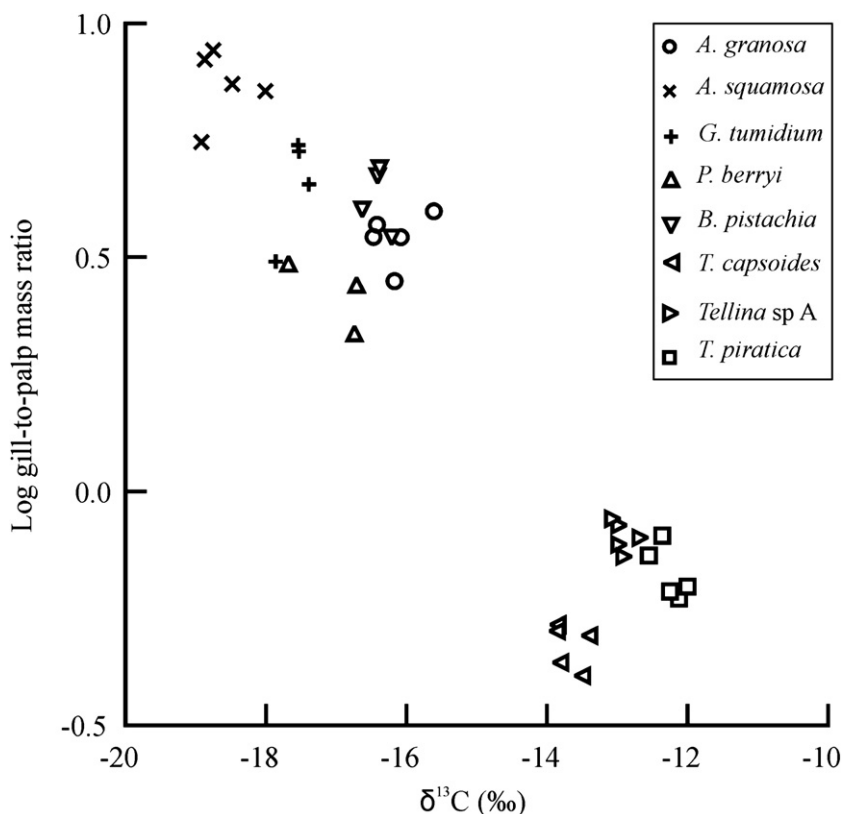
Values were calculated using the IsoSource mixing model by Phillips and Gregg (2003) using an increment of 1‰ and a tolerance of 0.1 per ml. Fractions of the oceanic plankton are abbreviated in the table: 250  $\mu\text{m}$  ( $X > 250 \mu\text{m}$ ), 110  $\mu\text{m}$  ( $250 \mu\text{m} > X > 110 \mu\text{m}$ ) and 60  $\mu\text{m}$  ( $110 \mu\text{m} > X > 60 \mu\text{m}$ ).

Notably, each species had a distinct carbon isotope signature (Fig. 2). In a single case, the lucinid bivalve (*D. irpex*) showed a depleted carbon isotope value of  $\delta^{13}\text{C}$  -23.1‰, as well as a depleted nitrogen isotope value of  $\delta^{15}\text{N}$  -0.9‰ (Fig. 2, Table 2).

The IsoSource model calculated the food source contributions to all bivalve species (Tables 3 and 4), except for the lucinid bivalve *D. irpex*. Notably, the model predicted that the suspension and deposit feeding bivalves were consuming very different proportions of available food sources in this system. Specifically, all suspension feeding species consumed a large proportion of mangrove material (average POM=24.6% and average leaf=24%). Only in two suspension feeders (*B. pistachia* and *A. squamosa*) was oceanic plankton, in combination with mangrove material, an important dietary component. In the

deposit feeding species, benthic diatoms were the most important diet component (average diatoms=31%). The second most important dietary component for the deposit feeders was the smallest plankton fraction in two species (*T. piratica* and *T. sp.*) or mangrove particulate organic matter in a single species (*T. capsoides*).

In this system, the carbon isotope signatures of bivalve species differed both between the suspension and deposit feeders and within each feeding mode (Fig. 3). Notably, in parallel with the clear differentiation of carbon isotope signatures, the log gill-to-palp mass ratios of the bivalves formed a gradient from suspension to deposit feeding (Fig. 3). This resulted in a significant correlation between the log gill-to-palp mass ratio and the carbon isotope signatures ( $R^2=0.85$ ,  $F_{1,34}=203$ ,  $P<0.01$ , Fig. 3).



**Fig. 3.** The relationship between the log gill-to-palp mass ratios and the carbon isotope signatures ( $\delta^{13}\text{C}$ ) is significant ( $R^2=0.85$ ,  $F_{1,34}=203$ ,  $P<0.01$ ), and shows a gradient of resource partitioning between the suspension and deposit feeding modes. The legend includes the species names.

#### 4. Discussion

In this study, carbon isotope signatures clearly distinguished differences in diet both within and between the suspension and deposit feeding bivalves at Roebuck Bay, northwest Australia. Differences in carbon isotope signatures within a single feeding mode are noticeable in species that were sampled within a small distance of each other, and thus where similar food resources should be available (Table 1, Fig. 1). Similar to other dietary studies using bivalves (Riera, 1998, 2007; Rossi et al., 2004), carbon signatures showed greater differences in diet than nitrogen signatures. The small differences in nitrogen isotope signatures suggest that all bivalves belong to the same trophic level, with the exception of *D. irpex*.

In this system, mangrove detritus and leaf material were the most important dietary components for all suspension feeders, and also an important component for the diet of the deposit feeders. The importance of mangrove detritus and leaf material to the diet of the bivalves is consistent with the close proximity of the bivalve species to the mangrove trees at Dampier flat and also One Tree (see Fig. 1). Furthermore, these results are supported by other studies that have shown plant organic matter can contribute to bivalve diets either directly (Peterson et al., 1985; Riera, 2007; Riera and Richard, 1997) or indirectly via trophic mediation by bacteria (Crosby et al., 1990; Langdon and Newell, 1990). In two suspension feeding bivalves (*B. pistachia*, *A. squamosa*) oceanic plankton was also an important dietary component. This is perhaps due to their physical location, which is further away from the mangroves than the other suspension feeders (Fig. 1). Consistent with the knowledge that deposit feeding bivalves gather their food from the surface of the sediment (Pohlo, 1967; Yonge, 1949), the deposit feeders in this study were mainly assimilating a diet of diatoms. In two of the three deposit feeders (*T. piratica* and *T. sp.*) the smallest plankton fraction ( $110\text{ }\mu\text{m} > x > 60\text{ }\mu\text{m}$ ) was also an important dietary component. Whether this planktonic food source was obtained directly from the water column or taken from the sediment surface is difficult to ascertain.

A third feeding mode, chemoautotrophy, was also identified at this system. In the lucinid species (*D. irpex*, Lucinidae) negatively depleted nitrogen and carbon isotope signatures identified the host as being a chemoautotroph, i.e. much of the host's carbon is supplied by endosymbiotic bacteria that obtain their energy from carbon dioxide fixation by the oxidation of reduced sulphur compounds (Dando et al., 1985; Rau, 1981). Note that the depleted nitrogen isotope ratios are expected to reflect the use of pore-water ammonium (Conway et al., 1989).

In parallel with the different carbon isotope signatures of the bivalves, the relative gill and palp sizes of the bivalves in this study fell along a gradient from suspension to deposit feeding. The strong correlation between the relative gill and palp sizes and carbon isotope signatures at this system suggest that either: (1) these species can select their diet, (2) they have different diets available to them, (3) a combination of (1) and (2), or (4) that there are differences in isotopic fractionation between species (Gannes et al., 1997; Tieszen et al., 1983). Because isotopic fractionation appears to be similar between the bivalve species studied so far (Dubois et al., 2007; Yokoyama et al., 2005), we do not consider fractionation accountable for the differences in isotopic signatures. Furthermore, as most species were sampled within a close proximity of each other (~250 m), and because the bay is well mixed as a result of large tidal ranges (~8 m), spatial variation in resources may only have a minimal impact on the carbon isotope signatures of the species. However, a spatial component might be present as two species living away from the mangroves, *B. pistachia* and *A. squamosa*, had a diet that contained a higher percentage of oceanic plankton. Nevertheless, the strong correlation between the relative size of the gills and palps and the carbon isotope signature of the bivalves strongly suggests that these feeding organs are involved in diet selection. Diet selection is consistent with the knowledge that bivalve species can sort qualitatively different food particles from a mixture using surface tracts on their gills and palps and by detection of the surface properties of the particles (Hemroth et al., 2000; Shumway and

Cucci, 1987; Shumway et al., 1985; Shumway et al., 1997; Ward et al., 1997). In addition, preingestive particle processing has also been related to the relative size of the gills and the palps, both within and between species (Dutertre et al., 2007; Velasco and Navarro, 2002).

As bivalve species are known to select their diet via a fine-tuned cooperation between their gills and palps (for review see Ward and Shumway, 2004), it is notable that a strong correlation between the gills and palps of the bivalve species and their carbon isotope signature, which reflects diet, was observed. In light of these results, the continuous gradient of relative gill and palp sizes between suspension and deposit feeders in Roebuck Bay (Compton et al., 2007) could suggest that bivalves select different diets from a shared pool of resources and thus decrease competition for food. Furthermore, the observation that relative gill and palp sizes in bivalves appear to be matched to diet suggests that bivalve feeding morphology is a unique functional trait for examining differences between species (Compton et al., 2007) and organismal performance (McGill et al., 2006).

#### Acknowledgements

For help in the field we thank H. Sombroek, K. Krans and R. de Jonge. We are grateful for the use of the facilities at the TAFE Aquaculture Centre and the Western Australian Fisheries laboratory via J. Bellanger in Broome. We thank the Broome Department of Environment and Conservation (DEC) office and the Broome Bird Observatory for their logistical support. This project was funded partly by Department of Conservation and Land Management's Wetland's Conservation grants program. TJC was funded by an Ubbo Emmius PhD Scholarship. We thank M.J.A. Rijkenberg, J. Drent, W.J. Wolff and two anonymous reviewers for their constructive comments on the manuscript. [SS]

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